Isolation and Characterization of Wheat-*Elymus* Addition, Substitution, and Translocation Lines

by

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INTRODUCTION

Perennial Triticeae grasses hold potential for broadening the genetic base and reducing the genetic vulnerability of common wheat (*Triticum aestivum* L., 2n = 6X = 42, genomes AABBDD). The *Agropyron* complex, composed of over 200 polyploid and diploid grasses, is perhaps the most worthy of exploitation. Genes from these species are accessible sources of barley yellow dwarf virus (BYDV), wheat streak mosiac virus (WSMV), leaf and stem rust resistance; and cold, drought, and salt tolerance (Cauderon 1979; Dewey 1984; Knott 1968; Sharma *et al.* 1984). Relatively few of these genes have been introgressed into wheat for crop improvement (Kibirige-Sebunya and Knott 1983; Knott *et al.* 1977; Larson and Atkinson 1973; Sears 1972; Sebesta *et al.* 1972; Sharma and Knott 1966; Wang *et al.* 1980). However, recent advances in wide hybridization and embryo rescue techniques have generated new hybrids between annual and perennial species of the Triticeae (Dewey 1984; Mujeeb-Kazi *et al.* 1987; Sharma and Gill 1983*b*).

The ability to produce intergeneric hybrids has opened the way for isolating disomic addition lines from complete alien genomes. O'Mara's (1940) discovery that individual rye chromosomes can be added to wheat led to similiar approaches in the isolation of addition lines of the perennial species. A complete set of wheat-*Elytrigia*

elongata (= Agropryon elongatum) addition lines and six wheat-*Thinopyrum intermedium (= Agropyron intermedium*) disomic addition lines have been produced (Cauderon *et al.* 1973; Hart and Tuleen 1983; Dvorak and Knott 1974).

Several approaches in the detection of addition lines have facilitated their isolation. The most powerful method has been the analysis of chromosome pairing in intercrossed hybrids between disomic addition lines (Dvorak and Knott 1974). Novel approaches include heterochromatin banding of karyotypes (Islam 1980; Jewell and Driscoll 1983; Singh and Tsuchiya 1982), and assays of structural genes by use of isozymes and DNA hybridization in southern blots (Gill *et al.* 1988; Hart *et al.* 1980).

Comprehensive genetic analyses of alien addition lines have numerous applications. With the use of aneuploids, the chromosomal location of genes have aided in the formulation of genetic linkage maps. Homoeologous relationships between wheat and alien chromosomes have been assayed through gametophytic and sporophytic compensation studies (Dvorak 1980; Dvorak and Chen 1984), and isozyme (Hart and Tuleen 1983) or DNA analyses (Gill *et al.* 1988). Such studies have added to our understanding of genome structure and phylogeny among the annual and perennial species of the Triticeae.

In our laboratory, the production of intergeneric hybrid, *Elymus trachycaulus (= Agropyron trachycaulum* 2n =

4x = 28, $S^tS^tH^tH^t$) X *T. aestivum cv.* Chinese Spring, initiated a wide hybridization program for the introgression of disease resistance from *Elymus* into wheat (Sharma and Gill 1981, 1983*a*). In the course of this program, backcross hybrids containing *Elymus* cytoplasm interacted with the wheat nucleus to give plant lethality in later generations. Only those plants which contained a critical *Elymus* chromosome(s) to overcome this lethal cytoplasmic effect were isolated as disomic addition lines (Sharma and Gill 1984). As a result, BC_1 and BC_2 derivatives were backcrossed as males with the recurrent wheat parent to obtain euplasmic hybrids.

In addition to the backcross program, comparative chromosome banding analysis provided evidence on the genomic evolution of *E. trachycaulus* and its diploid progenitor species. This study also identified the fourteen pairs of *Elymus* chromosomes and tentatively allocated each chromosome into the S^t or H^t genomes (Morris and Gill 1987). Isozyme and DNA assays provided preliminary evidence of homoeology from the location of structural genes on specific *Elymus* chromosomes (Gill *et al.* 1988; Raupp and Gill 1986, 1987). Collectively, these results have aided in the identification of new *Elymus* chromosomes added to wheat.

In the present paper, we report the isolation of new wheat-*Elymus* addition, substitution, and translocation

lines. The characterization of these lines was studied by means of morphological and chromosome pairing assays, and N-banding analyses. Genetic abnormalities such as nuclear-cytoplasmic effects and preferential transmission of specific *Elymus* chromosomes are discussed.

MATERIALS AND METHODS

Elymus trachycaulus was hybridized with *T. aestivum cv.* Chinese Spring with the former as the female parent (Sharma and Gill 1981, 1983*a*). Since a fertile amphiploid was never obtained, addition lines were isolated from a backcross program using BC_1, BC_2, and BC_3 derivatives developed by Sharma and Gill (1983*a*, 1984). Due to the incompatible effects of the *Elymus* cytoplasm, only a few alloplasmic addition lines with critical *Elymus* chromosomes were isolated. As an alternative approach, partially fertile 46-49 chromosome BC_1 and BC_2 hybrid plants were crossed as males with the recurrent wheat parent to obtain euplasmic hybrids. With continued backcrossing, the selection of monosomic addition lines followed.

Disomic addition lines (22") were produced most often by self-pollination of monosomic additions (21" + 1′), and in rare cases, in the progeny of 46 and 42-chromosome plants. Ditelosomic addition lines (21" + t") were obtained from self-pollination of monotelosomic additions

(21" + t') during the isolation of disomic additions. The substitution and translocation lines were detected by N-banding after their isolation. These lines were produced from 43-45 chromosome derivatives. All isolated lines originated from the same F_1 hybrid.

Due to rare transmission of *Elymus* chromosomes through the pollen of several monosomic addition lines, the *Hordeum bulbosum* method (Islam *et al.* 1981) was used to recover disomic additions. To obtain 22-chromosome haploids, monosomic additions were crossed as females with a *H. bulbosum* clone (2n = 28) selected for crossability. Haploid embryos were rescued 10-14 days after pollination and cultured on Murashige and Skoog (1962) media with supplements as described by Sharma and Gill (1983*a*). Haploid seedlings were treated with colchicine to double their chromosome number and recover disomic additions. The colchicine treatment followed the procedure of Pienaar (1981).

Using an incomplete diallel, several addition, substitution, and translocation lines were intercrossed to determine their identity and authenticity. The ditelosomic line was crossed with the disomic addition line from which it was isolated. The F_1 hybrids were grown and meiotic pairing analyzed. In several cases, meiotic N-banding was employed to observe the pairing behavior of specific chromosomes.

Detection of isolated lines was facilitated through somatic chromosome counts, N-banding analyses, and meiotic studies. For cytological examination, seeds were germinated in petri dishes on moistened filter paper. Root tips were harvested when 1-2 cm long and pretreated in ice water for 24 hr. Root tips for somatic counts and N-banding were fixed in 3:1 ethanol-acetic acid and kept at 22 +/- 2^{o}C for 2-3 days. Root tip squashes and the N-banding technique followed the procedure of Endo and Gill (1984) with slight modifications (slides for meiotic N-banding were placed in Giemsa stain for 10 min). For meiotic studies, spikes were fixed in Carnoy's solution (6:3:1, 95% ethanol-chloroform-acetic acid) for 48 h, and stored under refrigeration (5^{o}C) until further use. Individual anthers with pollen mother cells (PMCs) at metaphase I were squashed in 1% acetocarmine and cytologically examined.

The N-banded karyotypes of addition, substitution, and translocation lines were constructed as a means for chromosome identification. The *Elymus* chromosomes or translocations, either added or substituted in each line, were assigned the same designation as reported in the N-banded karyotype of *E. trachycaulus* (Morris and Gill 1987). In several cases, homoeology had been determined on the basis of biochemical and morphological markers, and therefore the designations of some *Elymus* chromosomes were changed. Wheat chromosomes 1A, 3D, 4D, 5D, and 6D could

not be identified by N-banding analysis and were therefore placed arbitrarily in each karyotype. Somatic metaphase chromosome length and arm ratios were determined from enlarged microphotographs of N-banded cells. Homologous chromosomes were measured in millimeters (mm) and averaged over 2-5 cells. To avoid differences in the degree of contraction, the average length of each chromosome was converted to microns (u) using 3B as a standard (13.8 u) as described in Endo and Gill (1984). The length of chromosomes in the parental species *E. trachycaulus*, was measured using disomic addition chromosome $1H^t$ as a standard (8.98 u). Arm ratios (long/short) were calcuated for homologous chromosomes and averaged over 2-5 cells. Microphotographs were taken with Kodak Tech Pan 2415 film using a Zeiss III photomicroscope. For printing, Kodak F5 and F4 Kodabromide papers were used.

Observations were recorded on plant vigor, fertility, height, morphological traits, spike characters, and disease resistance, and used to differentiate and describe each line. The number of seeds per spike from one to several plants was measured as an index of fertility. Morphological characters and mean plant height were determined from 1-5 plants. Photographs of plant spikes were taken with Kodak Panatomic-X film and printed on Kodak F3 Kodabromide paper.

RESULTS

N-banding analysis of addition, substitution, and translocation lines

The designation, cytoplasmic, and chromosome constitution of addition, substitution, and translocation lines are listed in Table 1. As described below, each line was designated on the basis of heterochromatin patterns, and biochemical and morphological markers.

In the disomic and ditelosomic addition lines, the presence of trisomics and translocations remained undetected by the N-banding technique. In several cases, *Elymus* chromatin could not be identified because of the lack of N-bands, therefore it was speculated that the alien segments were derived from the S^t genome in which some *Elymus* chromosomes are devoid of N-bands (Morris and Gill 1987).

In three disomic addition lines, the N-banding patterns of added *Elymus* chromosomes were identical to those of H^t1, H^t4, and H^t6 in the N-banded karyotype of *E. trachycaulus* (Morris and Gill 1987) (Figs. 1, 2, and 3). The designations of H^t1, H^t4, and H^t6 were replaced, however, as the gene synteny relationships were determined by means of molecular markers (Gill *et al.* 1988; Raupp *et al.* 1986, 1987). Genes for glutenin, gliadin, and alcohol dehydrogenase (Adh) were identified for disomic addition (DA) H^t1, and therefore changed as DA $1H^t$. Disomic

addition H^t4 was determined positive for glutamic-oxaloacetic transaminase (Got-2) and designated as DA $6H^t$. Group 5 homoeology for disomic addition H^t6 was predicted from location of 5S-DNA as well as genes for *B*-glucanase and shikimic dehydrogenase (Skdh-1). Therefore, the designation was changed to DA $5H^t$.

One disomic addition contained an added pair of *Elymus* chromosomes that were submetacentric, very tiny, and devoid of N-bands (Fig. 4). It was speculated that part of the chromosome had been deleted since it was much smaller than any chromosome of *E. trachycaulus* (Table 5). This addition line expressed a red coleoptile gene, and it was therefore designated as DA $7S^t$ deletion (del).

In two separate ditelosomic addition lines (Figs. 5 and 6), one pair of added *Elymus* telosomes were identical to $H1^tp$ and the other pair was similiar to H^t7p of *E. trachycaulus*. Ditelosomic addition H^t7p also expressed a red coleoptile gene. Genes controlling anthocyanin production have been located on the short arm of group 7 homoeologous chromosomes (Kuspira and Unrau 1958; Gale and Flavel 1971), therefore this line was designated ditelosomic addition $7H^tp$.

Several 42-chromosome alloplasmic lines contained wheat-*Elymus* translocations and were designated as disomic substitutions (DS). One alloplasmic line was identified as a disomic substitution for 7A in which a pair of unbanded

Elymus telosomes were translocated with a pair of long (q) arms of 7A (Fig. 7). This line was determined positive for acid phosphatase (Acph) (Raupp *et al.* 1986). Since the Acph gene is located on the q arm of wheat, the line was designated DS $4S^{t}q.7Aq(7A)$. Another line contained a pair of chromosomes with an unbanded telosome translocated with 7Ap, and another pair of chromosomes with an unbanded *Elymus* telosome translocated with 7Aq. One pair of these chromosomes were substituted for a pair of unbanded wheat chromosomes, which may have been either 1A, 3D, 4D, 5D, or 6D (Fig. 8). Group 1 homoeology was predicted from the location of a gene for gliadin (Raupp *et al.* 1987), therefore this line was designated as DS (?).7Ap(?) + $1S^{t}p.7Aq(?)$. Another alloplasmic line was identified as a disomic substitution for 5A in which part of the p arm of 5A was translocated with an unbanded segment from an *Elymus* chromosome (Fig. 9). This unknown *Elymus* segment was identified by meiotic studies as the distal end of $1H^{t}p$ (Tables 7 and 8). The line was therefore designated as DS $1H^{t}p$-5A(5A).

Several addition lines contained either a wheat-*Elymus* translocation or translocated chromosomes from the *Elymus* parent. One such line contained an added pair of chromosomes with unbanded *Elymus* telosome translocated with 7Aq (Fig. 10). Group 1 homoeology was predicted from the location of a gene for gliadin (Raupp *et al.* 1987),

therefore this line was designated DA $1S^tp.7Aq$. Disomic addition $1H^tp.7S^tp$ (Fig. 11) was identified in which the p arm of $1H^t$ was translocated with an unbanded *Elymus* telosome. This unknown alien segment was designated as $7S^tp$ because the line expressed a red coleoptile gene. Another translocation addition line contained either a pair of isochromosomes derived from $1H^tp$ or a pair of $1H^tp.H^t2q$ translocations (Fig. 12). Group 1 homoeology was predicted from the location of a gene for gliadin, and therefore the line was designated $1H^tp.(?)$. Also, disomic addition $1H^tp.5H^tq$ ($1H^tp$ translocated with $5H^tq$) and a double monoditelosomic line that contained one $1H^tp.(?)$ chromosome, one $1H^tp.5H^tq$ chromosome, and pair of telosomes of an unbanded *Elymus* chromosome were detected by N-banding (Figs. 13 and 14). In both lines, the identification of $1H^tp$ in the translocations was determined from the location of a gene for gliadin (Raupp *et al.* 1987).

Isolation of addition, substitution, and translocation lines

Alloplasmic disomic addition $1H^t$ was isolated in the BC_3F_2 generation from selfing a monosomic addition that contained 21" + 1′ at meiosis. In the progeny of the 43-chromosome derivative, 57.1% of the plants had 44 chromosomes (Table 2). This high frequency indicates that chromosome $1H^t$ may be preferentially transmitted through

the male and (or) female gametes. However, disomic addition (DTA) $1H^tp$ (alloplasmic) was produced in the BC_3F_3 generation at a lower (11.%) frequency from self-pollination of a 42 + t plant (Table 2). The N-banding technique also detected alloplasmic monotelosomic addition (MTA) $1H^tq$ after self-pollination of a 45-chromosome derivative. Since MTA $1H^tq$ was sterile (Fig. 16f), the ditelosomic addition line for $1H^tq$ could not be isolated so long as it contained the *Elymus* cytoplasm.

In the BC_4F_2 generation, euplasmic disomic addition $5H^t$ was isolated from the selfed progeny of a 46-chromsome plant containing $5H^t$, H^t2, a translocated 5B chromosome, and an extra unbanded chromosome added to the normal wheat chromosome complement (N-banding analysis). Although 3 progenies were analyzed, the frequency of recovered disomic additions was 66.6% (Table 2). This high frequency indicates a selective advantage for both male and female gametes carrying the extra $5H^t$ chromosome.

Euplasmic disomic addition $6H^t$ was derived from the BC_4F_3 generation and produced at a 11.1% frequency from self-pollination of a 43-chromosome derivative (Table 2).

Euplasmic ditelosomic addition $7H^tp$ was recovered at a 10.0% frequency in the BC_4F_3 generation from self-pollination of a 42 + t chromosome plant (Table 2). Due to low male transmission, isolation of disomic addition $7H^t$ proved unsuccessful through self-pollination of monosomic

addition (MA) $7H^t$ in the BC_4F_4 generation. Out of 50 selfed progeny, only 18.0% of the plants contained 43 chromosomes and the remaining 82.0% had 42 chromosomes. As a result, MA $7H^t$ was crossed as a female to *H. bulbosum* and one 22-chromosome haploid was recovered, which proved to be lethal.

Euplasmic disomic addition $7S^t$ del was developed through the *H. bulbosum* method after it was discovered that self-pollination of a monosomic addition line containing an unbanded *Elymus* chromosome (N-banding analysis) produced only 43 (27.3%) and 42 (72.6%) chromosome derivatives. From this progeny (BC_4F_3 generation), a 43-chromosome plant was crossed as a female to *H. bulbosum* and one 22-chromosome haploid was produced. Disomic addition $7S^t$ del was isolated after chromosome doubling of the 22-chromosome haploid. It is not known whether the deletion of $7S^t$ took place through the *H. bulbosum* method or in previous backcross generations.

Alloplasmic disomic substitution $1H^t$p-5A(5A) was isolated in the BC_5F_3 generation through self-pollination of a 44-chromosome derivative. Of the 4 progeny examined, 50.0% were DA $1H^t$p-5A(5A) and 50.0% were monosomic substitutions for $1H^t$p-5A(5A) (N-banding analysis) (Table 2). These data indicate that chromosome $1H^t$p- 5A(5A) was transmitted through the male and female gametes with the same frequency as 5A to produce DS $1H^t$p-5A(5A).

Alloplasmic disomic substitution $4S^tq.7Aq(7A)$ was produced in the BC_2F_3 generation from self-pollination of a 45-chromosome derivative, of which the identity of the added chromosomes is unknown. In the selfed progeny, 33.3% had 42 chromosomes, 33.3% contained 43 chromosomes, and 33.3% had 44 chromosomes (Table 2).

Alloplasmic disomic substitution (?).7Ap(?) + $1S^tp.7Aq(?)$ was isolated in the BC_3F_3 generation after selfing a 43-chromosome plant. In 10 selfed progeny, 60.0% had 42 chromosomes (fertile and vigorous), 30.0% had 42 chromosomes (sterile and weak growth), and 10.0% contained 43 chromosomes (Table 2). These data suggest that the 43-chromosome derivative may have contained a pair of (?).7Ap or $1S^tp.7Aq$ chromosomes already substituted for a pair of unbanded wheat chromosomes of the A or D genome. Unfortunately, meiotic analysis was not performed to determine if the disomic substitution contained a reciprocal translocation. Alloplasmic disomic addition $1S^tp.7Aq$ was produced in the BC_3F_5 generation from self-pollination of a 44-chromosome derivative. In the selfed progeny, 62.5% had 44 chromosomes and 37.3% contained 43 chromosomes (Table 2).

In the BC_4F_4 generation, euplasmic disomic addition $1H^tp.7S^tp$ was produced from self-pollination of a 43-chromosome derivative. Eight out of ten plants in the selfed progeny were analyzed by N-banding and found to be

DA $1H^tp.7S^tp$ (Table 2). These results indicate that chromosome $1H^tp.7S^tp$ is preferentially transmitted through the male and female gametes.

Alloplasmic disomic addition $1H^tp.(?)$ was isolated in both the BC_3F_4 and BC_3F_5 generations. Each line was derived from separate BC_2 hybrids containing 49 and 44 chromosomes, respectively. Disomic addition $1H^tp.(?)$ of the BC_3F_4 generation, was produced at a 11.1% frequency from self-pollination of a 43-chromosome derivative (Table 2). Moreover, 33.3% of the progeny with 42 chromosomes were vigorous and fertile. Disomic addition $1H^tp.(?)$ of the BC_3F_5 generation, was produced at a 16.6% frequency from self-pollination of a 42-chromosome derivative exhibiting vigor and fertility (Table 2). However, 33.3% of the progeny with 42 and 42 + t chromosomes were lethal. These results indicate that the 43 and 42-chromosome derivatives might be spontaneous monosomic substitutions in which the $1H^tp.(?)$ chromosome was substituted for an unknown wheat chromosome.

Disomic addition $1H^tp.5H^tq$ and the double monoditelosomic addition ($1H^tp.(?)$, $1H^tp.5H^tq$, and unidentified *Elymus* telosome pair) were both produced in the BC_5F_3 generation from self-pollination of a 44 + t-chromosome derivative. In the selfed progeny, 34.5% contained 44 chromosomes and only 3.45% had 44 + 2t chromosomes (Table 2).

Several lines were isolated that contained an unbanded *Elymus* chromosome (N-banding analysis) added to wheat. Attempts to isolate disomic addition lines through self-pollination of the 43-chromosome derivatives proved unsuccessful due to low transmission of the alien chromosome through the male pollen. In one case, self-pollination of a monosomic addition produced only 43 (20.0%) and 42 (80.0%) chromosome derivatives.

Meiotic analysis

The frequency and mean chromosome associations at first meiotic metaphase of the isolated lines are listed in Tables 3 and 4. The frequency of unpaired chromosomes was much greater in disomic $6H^t$ and $1H^tp.(?)$ when compared to the other lines (Table 4). These data show that these chromosomes, particularly $1H^tp.(?)$, may cause asynapsis. Evidence of meiotic pairing between wheat and *Elymus* chromosomes was not observed in the addition lines, with the exception of disomic addition $1S^tp.7Aq$. In this line, 30% of the PMC's showed 20" + 1 IV (ring quadrivalent) which indicates that the pair of $1S^tp.7Aq$ chromosomes share the same $1S^tp$ arm and are associated with 7A. In the double monoditelosomic addition ($1H^tp.(?)$, $1H^tp.5H^tq$, unidentified *Elymus* telosome pair), the lack of multivalents and the occurrence of 23" in 67% of the PMC's indicate that the telosomes are derived from a single

Elymus chromosome rather than a wheat chromosome. These results also show that translocations $1H^tp.5H^tq$ and $1H^tp.(?)$ share a common $1H^tp$ telosome since both chromosomes paired in 67% of the PMC's.

Chromosome lengths and arm ratios

In the addition lines, the mean chromosome lengths and arm ratios of $1H^t$, $5H^t$, and $6H^t$ showed little deviation from those of H^t1 ($1H^t$), H^t6 ($5H^t$), and H^t4 ($6H^t$) of *E. trachycaulus* (Table 5). Moreover, the arm ratios of $1H^t$, $5H^t$, and $6H^t$ were quite similar to the arm ratios of the respective group 1, 5, and 6 homoeologues of wheat (Endo and Gill 1984) (Table 5). This correlation provides further evidence of homoeology for the $1H^t$, $5H^t$, and $6H^t$ *Elymus* chromosomes.

There was little difference between the telosome lengths of $1H^tp$ and $7H^tp$ in the addition lines as compared to those of H^t1p and H^t7p of *E. trachycaulus* (Table 5). Furthermore, it was assumed that a deletion might have occurred in chromosome $7S^t$ when its mean chromosome length measured 4.72 u. This size deviates from S^t6 (7.75 u), the smallest *Elymus* chromosome (Tables 5 and 6).

In the remaining lines, mean chromosome lengths and arm ratios provided further evidence of translocations either added or substituted in the wheat complement (Table 6). The chromosome length and arm ratio of $1H^tp$-5A were strikingly different compared to those of chromosome 5A of

wheat (Endo and Gill 1984). In other substitution and addition lines, the arm ratios of translocated chromosomes $4S^tq.7Aq$, (?).7Ap, and $1S^t.7Aq$ were similiar, although the chromosome lengths did vary. There was, however, a slight difference in arm ratios between the 7A translocations and the normal 7A chromosome of wheat. The chromosome lengths and arm ratios of chromosomes $1H^tp.7S^tp$, $1H^tp.(?)$, and $1H^tp.5H^tq$ varied considerably from those of the *Elymus* chromosomes.

Meiotic analysis of intercrossed F_1 hybrids

A half diallel of intercrosses between all the isolated lines was not complete. However, the authenticity and identification of many lines were verified through meiotic analysis of the intercrossed F_1 hybrids listed in Tables 7 and 8.

At meiosis, the progenies from the cross DA $1H^t$ x DA $6H^t$ gave 21" + 2′ and 20" + 4′, thus confirming that $1H^t$ was different from DA H^t2 and DA $6H^t$. Moreover, meiotic N-banding of the DA $1H^t$ x DA $6H^t$ hybrid proved the authenticity of DA $1H^t$ and DA $6H^t$ (Fig. 15a). Meiotic analysis of the F_1 hybrid DA $1H^t$ x DA $1H^tp$ showed 21" + 1t" at a 75.0% frequency, and thus confirmed the identity of ditelosomic addition $1H^tp$. The identification of DS $1H^tp$-5A(5A) was also determined when the hybrid DA $1H^t$ x DS $1H^tp$-5A(5A) showed meiotic chromosome associations of 20" +

1"′ (52.0%), 21" + 1′ (37.0%), and 20" + 3′ (11.0%). In addition, meiotic N-banding revealed the association of $1H^t$, $1H^t$p-5A, and 5A chromosomes arranged in a trivalent (Fig. 15b). From these results, the translocation was known to contain a segment of $1H^t$p, which had lost a centromeric N-band, and 5A, which had lost the distal end of the short arm. The identification of DA $1H^t$p.$7S^t$p was also confirmed when it was crossed to DA $1H^t$ and DS $1H^t$p-5A(5A). At meiosis, the progenies from these crosses showed 22" (55%) and 19" + 1"′ + 2′ (15.0%), respectively, and thus confirmed that the short arm of the translocation was derived from $1H^t$p. Disomic substitution $4S^t$q.7Aq(7A) was crossed to disomic additions $1H^t$, $5H^t$, $6H^t$, and $1H^t$p.$7S^t$p , and in each hybrid, the chromosome associations were 21" + 1′, 20" + 3′, and 19" + 5′(observed only in the DA $1H^t$ x DS $4S^t$q.7Aq(7A) hybrid). Meiotic N-banding of the DA $1H^t$ x DS $4S^t$q.7Aq(7A) hybrid showed chromosome $4S^t$q.7Aq associated with the q arm of chromosome 7A in a rod bivalent (Fig. 15c). These results indicate that the translocated chromosome contains an alien segment other than $1H^t$, $5H^t$, $6H^t$, and $7S^t$p, and that the other arm is 7Aq. Disomic addition $1H^t$p.(?) was crossed to disomic additions $1H^t$, $1H^t$p, and $1H^t$p.$7S^t$p and in each hybrid, at least two univalents were observed. These results indicate that the $1H^t$p.(?) translocation may cause asynapsis since it was observed as a univalent in each hybrid.

Characterization of addition, substitution, and translocation lines

The sterile F_1 hybrid is characterized by extreme vigor, profuse tillering, and a perennial habit. The coleoptiles and culms are red, and the leaves and height are intermediate between Chinese Spring and *E. trachycaulus*. The spikes are awnletted (2-5mm) and slightly longer than Chinese Spring. Each addition, substitution, or translocation line have morphological features which distinguish them as different. Some lines have obvious characters of *E. trachycaulus*, while others are almost indistinguishable from Chinese Spring. The fertility and height data are provided in Figs. 18 and 19. Comparisons between spike morphology are illustrated in Figs. 16 and 17.

Disomic addition $1H^t$ and ditelosomic addition $1H^tp$ show reduced fertility, although DA $1H^t$ is almost sterile. The spikes of DA $1H^tp$ are as large and dense as Chinese Spring, while the spikes of DA $1H^t$ are smaller and less robust. The height is also greater for DA $1H^tp$ (107.5 cm) than for DA $1H^t$ (88.5 cm). These results suggest that genes for vigor are located on $1H^tp$. Comparisons between monotelosomic $1H^tq$ (sterile and weak growth) (Fig. 16f) and monotelosomic $1H^tp$ (fertile and vigorous) (Fig. 16g) indicate that genes compensating for the *Elymus* cytoplasm are also located on $1H^tp$. The addition lines appear to be

less stable than other lines and also show moderate resistance to powdery mildew and leaf rust (Appendix).

Disomic addition $5H^t$ is normal in vigor, but shows a reduction in fertility as compared to Chinese Spring. The spikes are larger than Chinese Spring, slightly awnletted, and very laxed. Disomic addition $5H^t$ shows moderate resistance to powdery mildew (Appendix).

Athough disomic addition $6H^t$ is extremly tall, characteristics such as vigor, habit, and fertility are indistinguishable from Chinese Spring. The spikes are similar in morphology except they are more dense.

Disomic addition $7S^t$ del is normal in vigor, but the fertility is slightly reduced as compared to Chinese Spring. The spikes are large, awnletted, and very dense approaching the top portion. Chromosome $7S^t$ del carries a red coleoptile gene and is moderately resistant to leaf rust (Appendix).

Ditelosomic addition $7H^tp$ is vigorous, produces many tillers with slender culms, and has a grass-like habit during the juvenile stage. Unlike Chinese Spring, the spikes are small, slender, tapering, and laxed. Ditelosomic addition $7H^tp$ is partially sterile, but more fertile than DA $1H^t$. Chromosome $7H^tp$ also carries a red coleoptile gene.

Although disomic substitution $1H^tp$-5A(5A) is quite vigorous, it shows a 50% reduction in fertility over

Chinese Spring. Disomic substitution $1H^tp$-5A(5A) flowers ten days earlier than Chinese Spring which may indicate that gene(s) affecting vernalization have been deleted from 5A. The spikes are short, dense, and compact. Since DS $1H^tp$-5A(5A) is alloplasmic, gene(s) compensating for the *Elymus* cytoplasm are located on the distal end of $1H^tp$. Also, this line is slightly unstable. Disomic substitution $1H^tp$-5A(5A) is moderately resistant to leaf rust (Appendix).

Disomic substitution $4S^tq$.7Aq(7A) is vigorous but shows reduced fertility as compared to Chinese Spring. Since this line is alloplasmic, chromosome $4S^t$ carries a gene(s) compensating for the *Elymus* cytoplasm on the q arm. Disomic substitution $4S^tq$.7Aq(7A) is resistant to the MAV (virus transmitted by *Macrosiphum avenae*) isolate of barley yellow dwarf virus (BYVD) (Appendix).

Disomic substitution (?).7Ap(?) + $1S^tp$.7Aq(?) and disomic addition $1S^tp$.7Aq are vigorous but also show reduced fertility. Both lines are alloplasmic and show partial fertility, therefore telosome $1S^tp$ contains a gene(s) which restores vigor and fertility when present in *Elymus* cytoplasm.

Characteristics such as vigor and fertility of disomic addition $1H^tp.7S^tp$ are indistinguisable from Chinese Spring. Interestingly, DA $1H^tp.7S^tp$ is much more fertile than DA $1H^t$, DA $1H^tp$, and DS $1H^tp$-5A(5A). This indicates

that the effect of Chinese Spring cytoplasm or the p arm of $7S^t$ influence fertility. The spikes are large, robust, awnletted, and very laxed. Disomic addition $1H^tp.7S^tp$ carries a red coleoptile gene on the p arm of $7S^t$. This line is slightly unstable and moderately resistant to leaf rust (Appendix).

Alloplasmic disomic addition $1H^tp.(?)$ is tall, vigorous, and as fertile as Chinese Spring. These results indicate that chromosome $1H^tp.(?)$ carries fertility restorer gene(s) which are present on both the $1H^tp$ and unidentified telosomes. It may be speculated that these genes produce a complemetary action which fully restore fertility. Disomic addition $1H^tp.(?)$ is unstable and shows moderate resistance to leaf rust (Appendix).

Disomic addition $1H^tp.5H^tq$ and the double monoditelosomic addition ($1H^tp(?)$, $1H^tp.5H^tq$, and unidentified *Elymus* telosome pair) are normal in vigor, but show reduced fertility. The spikes of each line are smaller and narrower than Chinese Spring.

DISCUSSION

The collection of wheat-alien addition lines from the perennial Triticeae have been limited to one diploid and one polyploid species belonging to the E genomes. Here we present the first comprehensive analysis of individual *E.*

trachycaulus ($S^tS^tH^tH^t$) chromosomes and telosomes either added or incorporated (as translocations) into the wheat genome. The karyotypic and chromosome pairing data indicate that at least seven *Elymus* chromosomes or telosomes of $1H^t$, $5H^t$, $6H^t$, $7H^t$, $1S^t$, $4S^t$, and $7S^t$ have been isolated. Preliminary evidence from N-banding and molecular assays (Gill *et al.* 1988, Morris and Gill 1987) indicate that these chromosomes may be allocated into either the S^t or H^t genomes.

The N-banding technique proved useful in determining the transmission rates of certain *Elymus* chromosomes in multiple and monosomic addition lines. In euplasmic monosomic or monotelosomic additions, the transmission frequencies of most *Elymus* chromosomes or telosomes ranged from 0% to 11% (Table 2). In this case, nontransmission or low transmission might be expected since the euploid pollen has a distict competitive advantage over any 22-chromosome pollen bearing the alien chromosome. In contrast, chromosomes $1H^t$, $5H^t$, and $1H^tp.7S^tp$ showed preferential transmission frequencies through the male and (or) female gametes. This is interesting since the addition lines for $1H^tp$ and $7S^t$ del were recovered at lower frequencies (Table 2). It is possible that the exclusive transmission of chromosome $1H^tp.7S^tp$ is controlled by gene(s) present in the p arm of $7S^t$ which have been deleted in disomic addition $7S^t$ del. The preferential transmission of

chromosome $1H^t$ may be controlled by gene(s) present only in the q arm. Kibirige-Subunya and Knott (1983) reported a similiar case in which chromosome $7el_2$ from *A. elongatum* was exclusively transmitted through the female gamete. As a result, all female gametes lacking the alien chromosome failed to function. Mann (1975) also found that a chromosome each from *Aegilops sharonensis* and *A. longissima* were exclusively transmitted through both male and female gametes. Chromosomes $1H^t$, $5H^t$, and $1H^tp.7S^tp$ may prove to have the same gametocidal action when present in wheat cytoplasm. If this is the case, new disomic addition lines may be difficult to isolate if either of these chromosomes are present in multiple addition lines.

Alloplasmic lines were recovered in which three different *E. trachycaulus* chromosomes compensated for the *Elymus* cytoplasm. Similiarly, the addition of critical *E. ciliaris (A. ciliare*, $S^cS^cY^cY^c$) chromosomes to the wheat genome restored fertility and vigor with *E. ciliaris* cytoplasm (Sharma and Gill 1984). Since *E. trachycaulus* and *E. ciliaris* share the S genome, it was speculated that the critical chromosomes might be derived from the same genome in both species. However, critical chromosome $1H^t$ of *E. trachycaulus* appears to have affinity for the H^t genome (Morris and Gill 1987) and thus far, only two critical chromosomes each from *E. trachycaulus* and *E. ciliarus* have been allocated into the S^t and S^c genomes (Gill *et al.*

1988). Of special interest, however, was the fact that both S^t and S^c genome chromosomes contain genes for Acph (Raupp *et al.* 1986). This provides evidence of group 4 homoeology for both chromosomes. Since homoeologous group 4 chromosomes of several *Aegilops* and *T. turgidum* species also carry cytoplasm-specific fertility genes (Joppa and Mann 1983; Mochizucki 1968), it might be speculated that such genes have played a role in polyploid speciation.

The genes which control nucleo-cytoplasmic interactions have differential effects on gamete function and embryo viability when present in different cytoplasms (Tsuji and Mann 1981) In this study, each critical chromosome ($1H^t$, $1S^t$, or $4S^t$) had varying effects on vigor and fertility restoration within the same *Elymus* cytoplasm. For example, disomic addition $1S^tp.7Aq$ showed increased fertility over disomic substitution $4S^tq.7Aq(7A)$ and disomic additions $1H^t$ and $1H^tp$. For chromosome $1H^t$, the gene(s) for vigor and fertility restoration appear to be located on the short arm. However, there was a reduction in compensating ability in disomic addition $1H^t$ as compared to ditelosomic addition $1H^tp$, which indicates a type of suppressive action within the whole chromosome. It was also interesting to note that disomic addition $1H^tp.(?)$ showed complete restoration of fertility as compared to other alloplasmic lines in which fertility was partially restored. It may be speculated that complementary fertility

restorer gene(s) are present in both $1H^tp$ and the unidentified arm of the translocation which results in complete restoration of fertility.

The occurrence of translocations was not uncommon since in many cases, aneuploid forms give rise to misdivision of univalents during meiosis. As a result, centromeric breakage and subsequent fusion of different telocentrics can occur. (Morris and Sears 1973). Dvorak and Chen (1984) detected translocations in several wheat-*Elytrigia* addition lines through gametophytic compensation studies, and Islam (1980) identified translocations in wheat-barley addition lines on the basis of N-banding. The interchanges reported in this study appear to be whole arm transfers between non-homoeologous chomosomes of wheat and *Elymus* (Figs. 7, 8, and 10) or between non-homoeologous chromosomes of *Elymus* (Figs. 11, 12, 13, and 14). Chromosome $1H^tp$-5A was an exception with interstitial break points occuring in the short arms of chromosomes $1H^t$ and 5A (Fig. 9). Also, throughout the isolation of addition lines a number of deletions were detected in wheat chromosomes, especially within the B genome. These abberations may reflect genetic interactions between the *Elymus* and *Triticum* chromosomes.

Biochemical markers (Gill *et al.* 1988, Raupp *et al.* 1986, 1987) and N-banding proved essential for determining which *Elymus* chromosomes or translocations had been added

or substituted into wheat. Since the biochemical markers indicate genetic similarities among wheat and *Elymus* homoeologues, it would seem probable that *Elymus* chromosomes would simulate the effects of tetrasomy for corresponding wheat homoeologues. Sears (1968) observed that wheat-rye addition lines for group 2 closely resembled group 2 Chinese Spring tetrasomics in having increased awn length, slender culms, narrower leaves, and stiffer glumes. In this study, euplasmic disomic addition $6H^t$ was the only line which resembled the corresponding group 6 Chinese Spring tetrasomics in which fertility and spikes morphology appeared close to normal (Sears 1954) (Fig. 16i and Table 9). Morphological differences in the remaining disomic additions may be attributed to the expression of genes from specific *Elymus* chromosomes, or nucleo-cytoplamic interactions as in the case of disomic addition $1H^t$.

Increased spike length, laxed internodes, and the presence of awnlettes were dominant traits observed in *E. trachycaulus* and the sterile F_1 hybrid. These spike characters were also observed in disomic additions $5H^t$, $7S^t$ del, and $1H^t$p.$7S^t$p (Figs. 16i, 17b, and 17e). A similar pattern was found for wheat-*Elytrigia* addition lines in which the genes for spike length were distributed on several *Elytrigia* chromosomes related to groups 2 and 7 (Dvorak and Knott 1974; Dvorak 1980). It is probable that such traits are quantitative and are broken down during the

isolation of alien chromosomes in addition lines.

Genes controlling anthocyanin production have been located on *Ae. squarrosa* chromosome 7D (Jha 1964), *E. elongata* chromosome 7E (Dvorak 1974), and on wheat chromosomes 7A (Kuspira and Unrau (1958) and 7B (Gale and Flavell 1971). Similarly, chromosomes $7H^t$ and $7S^t$ carry genes for red coleoptile which provides evidence for group 7 homoeology. In addition, genes for disease resistance have been located on chromosomes $1H^t$, $5H^t$, $4S^t$, and $7S^t$ (Appendix). This was interesting since the same chromosomes either compensated for the *Elymus* cytoplasm or showed preferential transmission in the male or female gametes.

Estimates of fertility for disomic additions $6H^t$ and $1H^tp.(?)$ indicate that increased fertility may be due to genes specific to the donor *Elymus* species (Fig. 18). However, reduced fertility could be attributed to a number of genetic factors. As Sears (1954) pointed out, many wheat tetrasomics show a reduction in fertility, so it may be that increased dosages of genes on alien chromosomes have an effect on fertility. Dvorak and Knott (1974) reported a similiar case in which wheat-*Elytrigia* addition lines showed reduced fertility. Moreover, nucleo-cytoplasmic effects may also influence reduced fertility as in the case of disomic additions $1H^t$, $1H^tp$, and $1S^tp.7Aq$ and disomic substitutions $4S^tq.7Aq(7A)$ and (?).7Ap(?) +

$1S^{t}p.7Aq(?)$ (Fig. 18).

The meiotic and breeding behavior of the addition lines indicate the degree to which the *Elymus* chromosomes integrate into the genetic system of wheat and also influence the ease with which the lines can be maintained. The isolated lines exhibited normal pairing behavior with the exception of disomic additions $6H^{t}$ and $1H^{t}p.(?)$ which showed reduced pairing. From Table 3, both lines had a range of 0 to 2 univalents indicating that asynapsis is probably due to lack of pairing between the *Elymus* chromosomes. It is possible that the gene(s) that promote asynapsis in chromosome $1H^{t}p.(?)$ are located on the unidentified arm because in disomic additions $1H^{t}$ and $1H^{t}p$ normal pairing was observed. This speculation may explain the reason for the lack of pairing between chromosome $1H^{t}p.(?)$ and chromosomes $1H^{t}$, $1H^{t}p$, or $1H^{t}p.7S^{t}$ in the progenies of the F_1 hybrids. Moreover, it is likely that genetic factors are more important in determining fertility rather than chromosome pairing since disomic addition $1H^{t}p.(?)$ was most fertile and showed the greatest meiotic irregularity. Addition and substitution lines which involved chromosome $1H^{t}$ appear to be unstable which makes it essential to determine the chromosome constitution in each generation to maintain the integrity of each line.

The combination of cytological methods demonstrated in this study should prove useful in future experiments aimed

at the isolation of a complete set of wheat-*Elymus* addition lines. Apart from this objective, the chromosomal location of morphological and biochemical markers will provide new insight into the gene synteny relationships between wheat and *Elymus* chromosomes. This information will be helpful by indicating which wheat and *Elymus* chromosomes to include in gametophytic and sporophytic compensation studies. Finally, new sources of resistance to leaf rust and barley yellow dwarf virus have been identified in translocated chromosomes $1H^{t}p$-5A and $4S^{t}p$.7Aq, repectively. Since the resistance has already been incorporated into the wheat genome, these translocations may prove useful for the development of disease resistant germplasm.

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TABLE 1. Designation, cytoplasmic, and chromosome constitution of disomic, ditelosomic, substitution, and translocation lines of *Elymus trachycaulus* chromosomes added to Chinese Spring wheat.

Isolated line[a]	Cytoplasmic and chromosome constitution[b]
DA $1H^t$	Alloplasmic. 21" + $1H^t$".
DA $1H^t$p	Alloplasmic. 21" + $1H^t$p".
DA $5H^t$	Euplasmic. 21" + $5H^t$".
DA $6H^t$	Euplasmic. 21" + $6H^t$".
DA $7H^t$	Euplasmic. 21" + $7H^t$".
DA $7H^t$p	Euplasmic. 21" + $7H^t$p".
DA $1S^t$	Euplasmic. 21" + $1S^t$".
DA $7S^t$ del	Euplasmic. 21" + $7S^t$". 7S contains a deletion.
DS $1H^t$p-5A(5A)	Alloplasmic. 20" + 1Hp-5A". Nullisomic for most of 5Ap.
DS $4S^t$q.7Aq(7A)	Alloplasmic. 20" + $4S^t$q.7Aq". Nullisomic for 7Ap.
DS (?).7Ap(?) + $1S^t$p.7Aq(?)	Alloplasmic. 19" + (?).7Ap" + $1S^t$p.7Aq". Nullisomic for unidentified wheat chromosome.
DA $1S^t$p.7Aq	Alloplasmic. 21" + $1S^t$p.7Aq". Tetrasomic for 7Aq.
DA $1H^t$p.$7S^t$p	Euplasmic. 21" + $1H^t$p.$7S^t$p".
DA $1H^t$p(?)	Alloplasmic. 21" + $1H^t$p.(?)".
DA $1H^t$p.$5H^t$q	Euplasmic. 21" + $1H^t$p.$5H^t$q".
DMTA $1H^t$p$_t$(?), $1H^t$p.$5H^t$q, unidentified *Elymus* telosome pair	Euplasmic. 21" + $1H^t$p.(?)' + $1H^t$p.$5H^t$q' + t".

TABLE 1. (cont.)

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[a] DA = disomic addition, DS = disomic substitution, DMTA = double monoditelosomic addition, the nullisomic wheat chromosome indicated in parentheses.

[b] Alloplasmic cytoplasm from *Elymus trachycaulus*, euplasmic cytoplasm from Chinese Spring wheat, each formula indicates 21 pairs (21"), 20 pairs (20"), or 19 pairs (19") of Chinese Spring wheat chromosomes followed by addition of indicated chromosome pair or single chromosome.

Table 2. Mean frequencies of recovered disomic, ditelosomic, substitution, and translocation lines from selfed-backcross derivatives of Elymus trachycaulus x Chinese Spring wheat crosses.

Isolated line	Pedigree[a]	Chr. no. of backcross derivative	No. progeny examined	No. of plants with the indicated chromosome constitution				
				42	42 + t	42 + 2t	43	44
DA $1H^t$	BC_3F_2	43	7		2		1	4
[b]DA $1H^t$p	BC_3F_3	42 + t	9	3	4	1		
[c]DA $5H^t$	BC_4F_2	46	3					2
DA $6H^t$	BC_4F_3	43	9	4			3	1 (DM[d])
DA $7H^t$p	BC_4F_3	42 + t	10	9		1		1 (DA)
[d]MA $7H^t$	BC_4F_4	43	50	41			9	
[e]DA $7S^t$ del	BC_4F_3	43	11	8			3	
DS $1H^t$p-5A(5A)	BC_5F_3	44	4	2 (MS[d]) 2 (DS)				
DS $4S^t$q.7Aq(7A)	BC_2F_3	45	3	1			1	1
DS (?)$1S^t$p.7Ap(?), $1S^t$p.7Aq(?)	BC_3F_3	43	10	6 3 (lethal)			1	
DA $1S^t$p.7Aq	BC_3F_5	44	8				3	5
DA $1H^t$p.$7S^t$p	BC_4F_4	43	10					10
DA $1H^t$p.(?)	BC_3F_4	43	9	3			5	1
DA $1H^t$p.(?)	BC_3F_5	42	6	1 (lethal)	1 (lethal)		3	1
[f]DA $1H^t$p.$5H^t$q	BC_5F_3	44 + t	29					10
[f]DMTA $1H^t$p.(?), $1H^t$p.$5H^t$q, unidentified Elymus telosome pair	BC_5F_3	44 + t	29					10

[a] Indicates number of backcross (BC_2-BC_5) and selfed (F_2-F_5) generations.
[b] Other progeny recovered: 41 + t (1).
[c] Other progeny recovered: 45 (1).
[d] DM = double monosomic, MA = monosomic addition, MS = monosomic substitution.
[e] DA $7S^t$ del recovered from the Hordeum bulbosum method.
[f] Other progenies recoverd: 43 + t (1), 44 + t (15), 45 + t (2), 44 + 2t (1).

Table 3. Mean chromosome associations at meiotic metaphase I of addition, substitution, and translocation lines. Range of chromosome associations are given in parentheses.

Isolated line	Chr. no.	No. of PMC's examined	Metaphase I chromosome associations		
			univalents	bivalents rod	bivalents ring
DA $1H^t$	44	30	0.03 (0-2)	2.77 (1-5)	19.20 (17-21)
DA $1H^tp$	42 + 2t	6	0.00 (0)	3.17 (0-6)	18.80 (16-21)
DA $5H^t$	44	29	0.13 (0-2)	2.44 (0-5)	19.88 (17-22)
DA $6H^t$	44	20	0.30 (0-2)	2.55 (0-6)	19.30 (15-22)
DA $7H^tp$	42 + 2t	20	0.00 (0)	2.60 (1-5)	19.40 (16-21)
DA $7S^t$ del	44	20	0.20 (0-2)	2.30 (1-6)	19.60 (16-21)
DS $1H^tp$-5A(5A)	42	12	0.17 (0-2)	1.17 (0-3)	19.50 (18-21)
DS $4S^tq$.7Aq(7A)	42	18	0.10 (0-2)	2.40 (1-4)	18.60 (16-20)
[a]DA $1S^tp$.7Aq	44	20	0.05 (1)	1.05 (0-3)	20.25 (18-22)
DA $1H^tp$.$7S^tp$	44	13	0.00 (0)	1.60 (0-4)	20.40 (18-22)
DA $1H^tp$.(?)	44	10	0.80 (0-2)	2.10 (0-4)	19.40 (18-21)
DA $1H^tp$.$5H^tq$	44	10	0.00 (0)	2.70 (1-5)	19.30 (17-21)
DMTA $1H^tp_t$(?), $1H^tp$.$5H^tq$, unidentified *Elymus* telosome pair	44 + 2t	12	0.83 (0-4)	4.33 (2-7)	17.83 (15-21)

[a] Multivalents, 0.05 (0-1) III and 0.03 (0-1) IV, were also observed.

Table 4. Frequency of chromosome associations at meiotic metaphase I of addition, substitution, and translocation lines.

Isolated line	Chr. no.	No. of PMC's examined	Metaphase I chromosome associations			
			22"	21" + 2'	21"	20" + 2'
DA $1H^t$	44	30	0.97	0.03		
DA $1H^tp$	42 + 2t	6	1.00			
DA $5H^t$	44	29	0.97	0.03		
DA $6H^t$	44	20	0.85	0.15		
DA $7H^tp$	42 + 2t	20	1.00			
DA $7S^t$ del	44	20	0.90	0.10		
DS $1H^tp$-5A(5A)	42	12			0.92	0.08
DS $4S^tq$.7Aq(7A)	42	18			0.94	0.06
[a]DA $1S^tp$.7Aq	44	20	0.65			
DA $1H^tp$.$7S^tp$	44	13	1.00			
DA $1H^tp$.(?)	44	10	0.60	0.40		
DA $1H^tp$.$5H^tq$	44	10	1.00			
[b]DMTA $1H^tp$.(?), $1H^tp$.$5H^tq$, unidentified Elymus telosome pair	44 + 2t	12				

[a] Other associations include: 20" + 1 IV (0.30) and 19" + 1 "' + 1' (0.05).
[b] Associations include: 23" (0.67), 22" + 2' (0.25), and 21" + 4' (0.08).

Table 5. Mean chromosome lengths and arm ratios of Elymus trachycaulus chromosomes and Elymus chromosomes of disomic and ditelosomic addition lines. Arm ratios of several wheat chromosomes are also presented[a].

Elymus chromosome	Elymus trachycaulus		Disomic or ditelosomic addition lines		Arm ratios of wheat homoeologues
	Length in u	Arm ratio	Length in u	Arm ratio	
H^t1 ($1H^t$)	8.98	1.82	8.98	1.74	1A (1.9), 1B (1.7), 1D (1.7)
H^t1p ($1H^tp$)	3.22		3.34		
H^t2	10.34	1.21			
H^t3	12.06	1.47			
H^t4 ($6H^t$)	9.49	1.16	8.85	1.19	6A (1.1), 6B (1.2), 6D (1.2)
H^t5	10.92	1.41			
H^t6 ($5H^t$)	10.00	2.01	9.21	2.09	5A (1.8), 5B (2.0), 5D (1.9)
H^t7	11.63	1.01			
H^t7p ($7H^tp$)	5.72		5.13		
S^t1	11.07	1.11			
S^t2	10.91	1.69			
S^t3	9.60	1.05			
S^t4	9.31	1.34			
S^t5	11.42	2.05			
S^t6	7.75	1.16			
S^t7	11.87	1.16			

[a] Arm ratio data taken from Endo and Gill (1984).

Table 6. Mean chromosome lengths and arm ratios of the $7S^t$ and translocated chromosomes. Chromosome lengths and arm ratios of wheat chromosomes 5A and 7A are also presented[a].

Abberant chromosome	Length in u	Arm ratio	Wheat Chr.	Length in u	Arm ratio
$7S^t$ del	4.72	1.64			
$1H^tp$-5A	9.06	3.53	5A	11.5	1.8
$4S^tq$.7Aq	10.35	1.29	7A	11.3	1.0
[b](?).7Ap	11.75	1.24	7A	11.3	1.0
[b]$1S^tp$.7Aq	11.27	1.25	7A	11.3	1.0
[c]$1S^tp$.7Aq	11.41	1.21	7A	11.3	1.0
$1H^tp.7S^tp$	8.08	1.61			
$1H^tp$.(?)	6.53	1.10			
$1H^tp.5H^tq$	10.45	1.92			

[a] Data taken from Endo and Gill (1984).
[b] Chromosome from disomic substitution (?).7Ap(?) + $1S^tp$.7Aq(?).
[c] Chromosome from disomic addition $1S^tp$.7Aq.

Table 7. Mean chromosome associations at meiotic metaphase I of the intercrossed F1 hybrids. Range of chromosome associations are given in parentheses.

Intercross	Chr. no.	No. of PMC's examined	Metaphase I chromosome associations		
			univalents	bivalents rod	bivalents ring
$1H^t$ x $6H^t$	44	20	2.10 (2-4)	2.25 (0-6)	18.70 (15-21)
[a] $1H^t$ x $1H^tp$	43 + t	8	0.75 (2-4)	2.88 (1-6)	17.75 (14-19)
$1H^t$ x DS $4S^tq.7Aq(7A)$	43	20	1.80 (1-5)	3.55 (1-9)	17.05 (12-20)
[b] $1H^t$ x DS $1H^tp$-5A(5A)	43	35	0.70 (0-3)	1.89 (0-5)	18.37 (15-21)
$1H^t$ x $1H^tp.7S^tp$	44	20	1.20 (0-4)	3.90 (1-8)	17.50 (15-20)
$6H^t$ x DS $4S^tq.7Aq(7A)$	43	20	1.60 (1-5)	3.30 (2-6)	17.40 (15-19)
$6H^t$ x DS $1H^tp$-5A(5A)	43	20	1.80 (1-5)	2.65 (0-5)	17.85 (15-20)
$6H^t$ x $1H^tp.7S^tp$	44	20	2.00 (2)	1.75 (0-4)	19.25 (17-21)
$5H^t$ x DS $4S^tq.7Aq(7A)$	43	30	1.30 (1-3)	3.30 (1-9)	17.57 (12-20)
$5H^t$ x DS $1H^tp$-5A(5A)	43	20	1.40 (1-3)	3.35 (0-8)	17.45 (13-21)
$5H^t$ x $1H^tp.7S^tp$	44	15	2.13 (2-4)	2.40 (0-5)	18.53 (16-21)
$1H^tp.7S^tp$ x DS $4S^tq.7Aq(7A)$	43	20	1.10 (1-3)	2.35 (1-4)	18.60 (17-20
[c] $1H^tp.7S^tp$ x DS $1H^tp$-5A(5A)	43	20	0.50 (0-2)	2.30 (0-5)	17.75 (15-20)
$1H^tp.(?)$ x $1H^t$	44	15	2.53 (2-4)	2.80 (0-7)	17.93 (14-21)
$1H^tp.(?)$ x $1H^tp$	43 + t	12	2.00 (1)	3.17 (2-4)	17.83 (17-19)
$1H^tp.(?)$ x $1H^tp.7S^tp$	44	20	2.00 (2)	3.50 (1-5)	17.55 (16-20)

[a] Heteromorphic bivalent, 1.00 (1) II, was observed.
[b] Trivalent, 0.60 (0-2), was observed.
[c] Trivalent, 0.80 (0-1), was observed.

Table 8. Frequency of chromosome associations at meiotic metaphase I of the intercrossed F1 hybrids.

Intercross	Chr. no.	No. of PMC's examined	Metaphase I chromosome associations				
			21" + 2'	20" + 4'	21" + 1'	20" + 3'	19" + 5'
$1H^t \times 6H^t$	44	20	0.95	0.05			
[a] $1H^t \times 1H^tp$	43 + t	8					
$1H^t \times$ DS $4S^tq.7Aq(7A)$	43	20			0.65	0.30	0.05
[b] $1H^t \times$ DS $1H^tp$-5A(5A)	43	35			0.372	0.114	
[c] $1H^t \times 1H^tp.7S^tp$	44	20	0.30	0.15			
$6H^t \times$ DS $4S^tq.7Aq(7A)$	43	20			0.75	0.20	0.05
$6H^t \times$ DS $1H^tp$-5A(5A)	43	20			0.65	0.30	0.05
$6H^t \times 1H^tp.7S^tp$	44	20	1.00				
$5H^t \times$ DS $4S^tq.7Aq(7A)$	43	30			0.83	0.17	
$5H^t \times$ DS $1H^tp$-5A(5A)	43	20			0.80	0.20	
$5H^t \times 1H^tp.7S^tp$	44	15	1.00				
$1H^tp.7S^tp \times$ DS $4S^tq.7Aq(7A)$	43	20			0.95	0.05	
[d] $1H^tp.7S^tp \times$ DS $1H^tp$-5A(5A)	43	20			0.20		
[e] $1H^tp.(?) \times 1H^t$	44	15	0.80	0.13			
$1H^tp.(?) \times 1H^tp$	43 + t	12	1.00				
$1H^tp.(?) \times 1H^tp.7S^tp$	44	20	1.00				

[a] Chromosome associations, 21" + 1t" (0.75), 20" + 1t" + 2'(0.125), and 19" + 1t" + 4'(0.125).
[b] Additional chromosome association, 20" + 1"' (0.514).
[c] Additional chromosome association, 22" (0.55).
[d] Additional chromosome associations, 20" + 1"' (0.65), 19" + 1"' + 2' (0.15).
[e] Additional chromosome association, 19" + 6' (0.07).

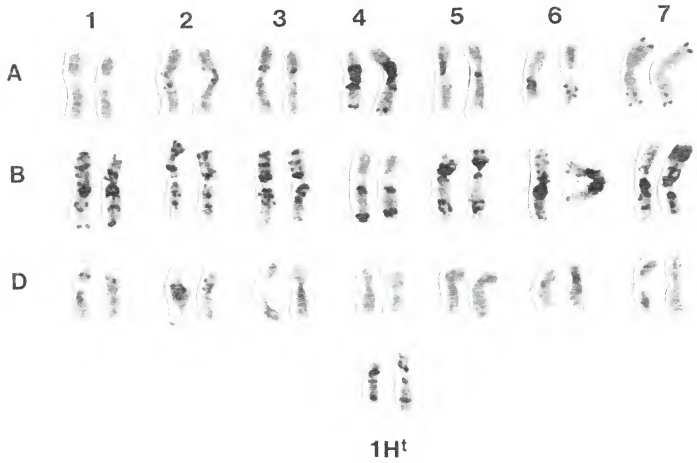


Fig. 1. N-banded karyotype of disomic addition $1H^t$.

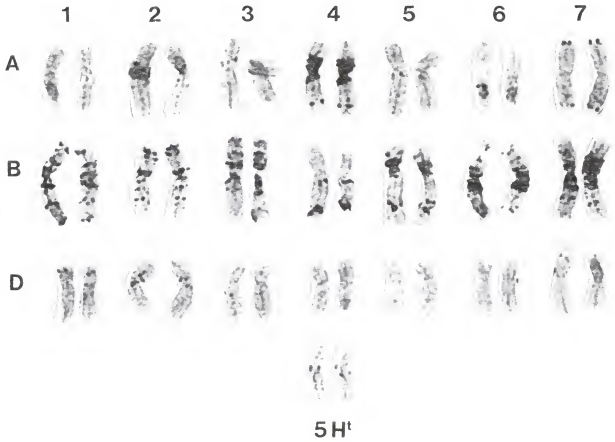


Fig. 2. N-banded karyotype of disomic addition 5H^t.

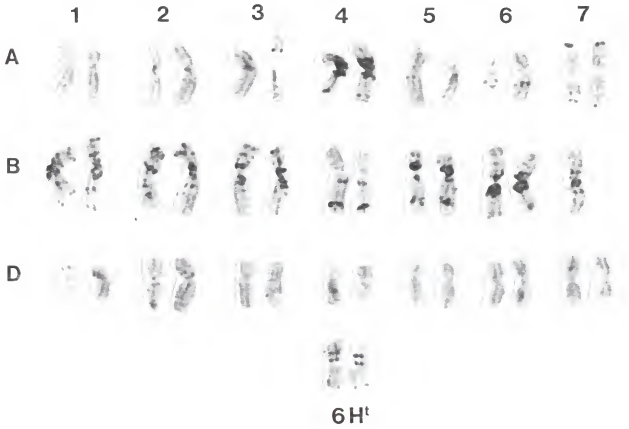


Fig. 3. N-banded karyotype of disomic addition 6H^t.

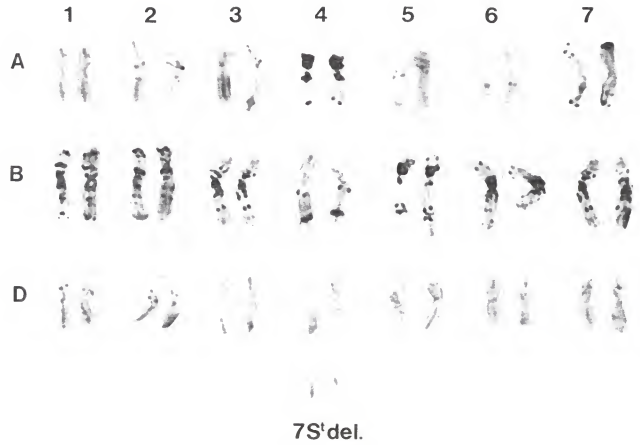


Fig. 4. N-banded karyotype of disomic addition 7S' del.

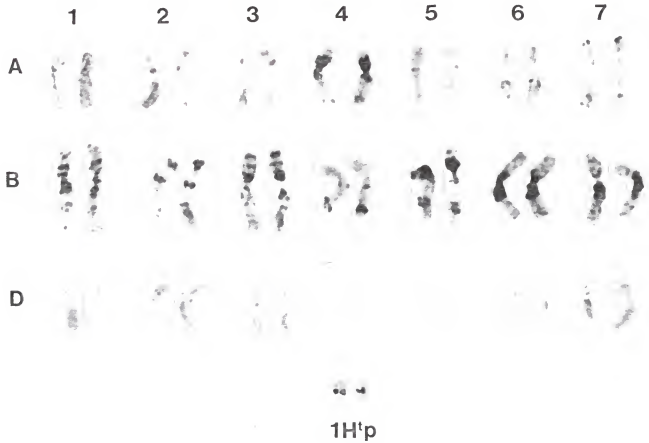


Fig. 5. N-banded karyotype of ditelosomic addition 1H^tp.

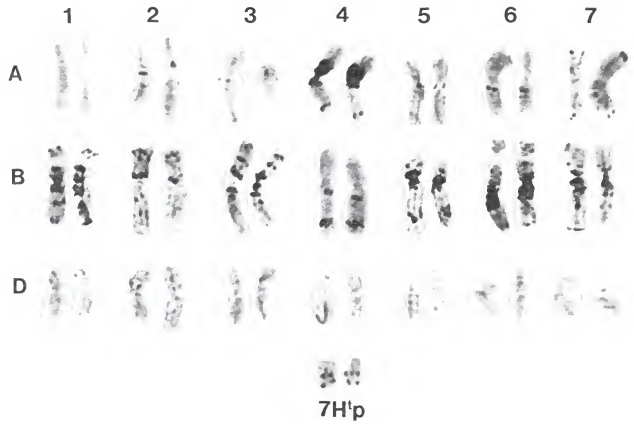


Fig. 6. N-banded karyotype of ditelosomic addition 7H^tp.

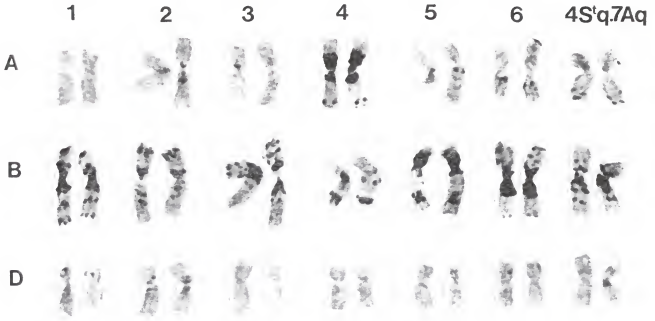


Fig. 7. N-banded karyotype of disomic substitution 4S^{t}q.7Aq(7A).

Fig. 8. N-banded karyotype of disomic substitution (?).7Ap(?), 1S'p.7Aq(?). Trisomic for 4A.

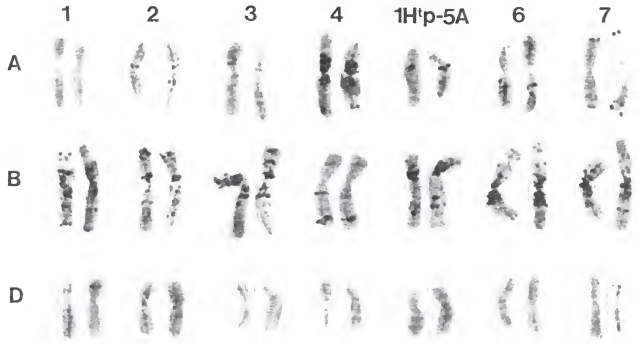


Fig. 9. N-banded karyotype of disomic substitution 1H^tp-5A(5A).

Fig. 10. N-banded karyotype of disomic addition 1S'p.7Aq.

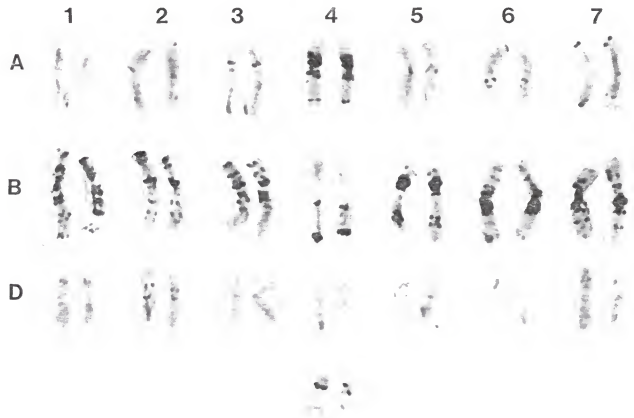


Fig. 11. N-banded karyotype of disomic addition 1H^tp.7S^tp.

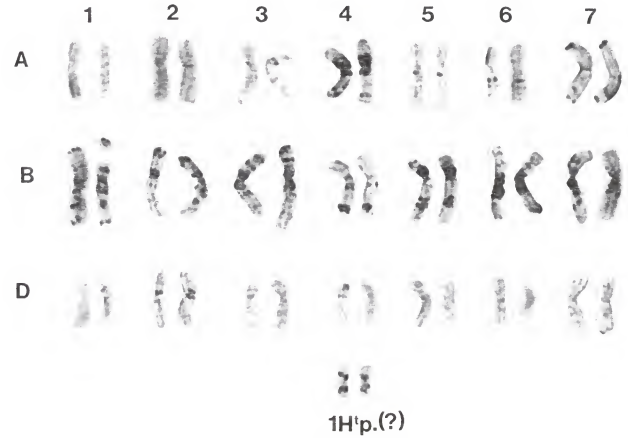


Fig.12. N-banded karyotype of disomic addition 1H^l p.(?)

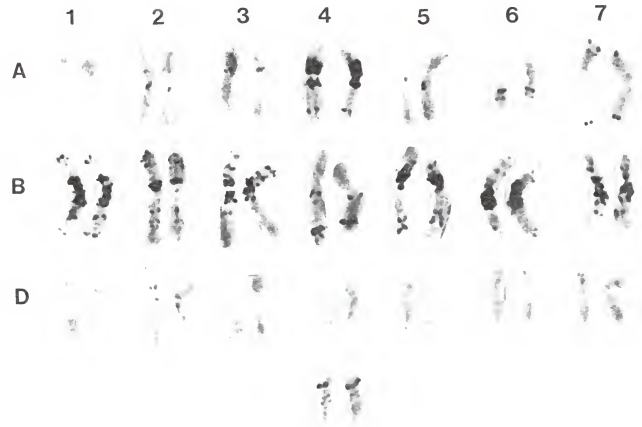


Fig. 13. N-banded karyotype of disomic addition 1H^t p.5H^t q.

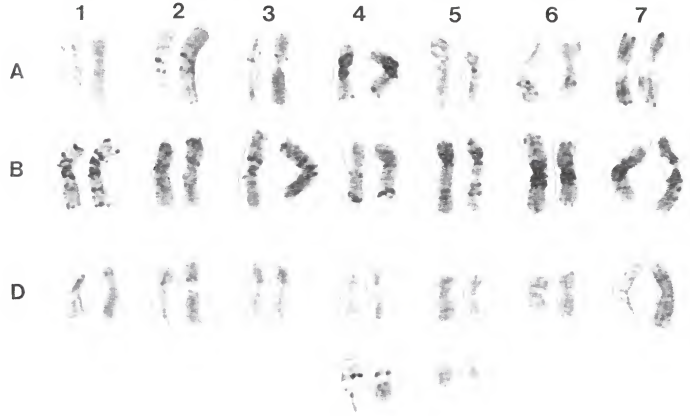


Fig. 14. N-banded karyotype of double monoditelosomic addition $1H^{l}p.5H^{l}q$, $1H^{l}p.(?)$, and unidentified Elymus telosomes.

Figure 15. Meiotic N-banding of intercrossed F_1 hybrids. (a) Disomic addition $1H^t$ x disomic addition $6H^t$, showing $1H^t$ and $6H^t$ univalents. (b) Disomic addition $1H^t$ x disomic substitution $1H^tp$-5A(5A), chromosomes $1H^t$, $1H^tp$-5A, and 5A paired in a trivalent. (c) Disomic addition $1H^t$ x disomic substitution $4S^tq.7Aq(7A)$, chromosomes 7A and $4S^tq.7Aq$ paired in a rod bivalent.

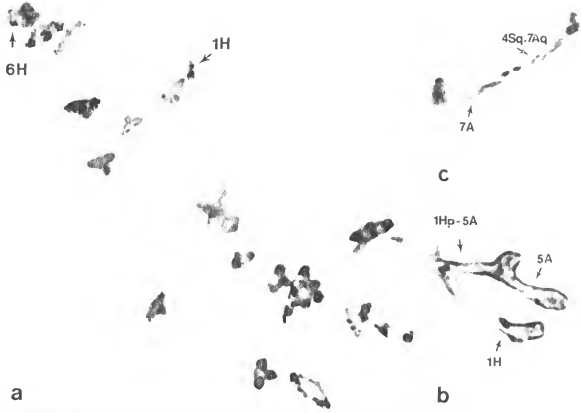

6H
1H
a
4Sq.7Aq
7A
c
1Hp-5A
5A
1H
b

Figure 16. Spike morphology of (a) Elymus trachycaulus, (b) F_1 hybrid, (c) Chinese Spring wheat, (d) disomic addition $1H^t$, (e) disomic addition $1H^tp$, (f) monotelosomic addition $1H^tq$, (g) monotelosomic addition $1H^tp$, (h) addition $1H^tp$.(?), (i) disomic addition $6H^t$, (j) disomic addition $5H^t$.

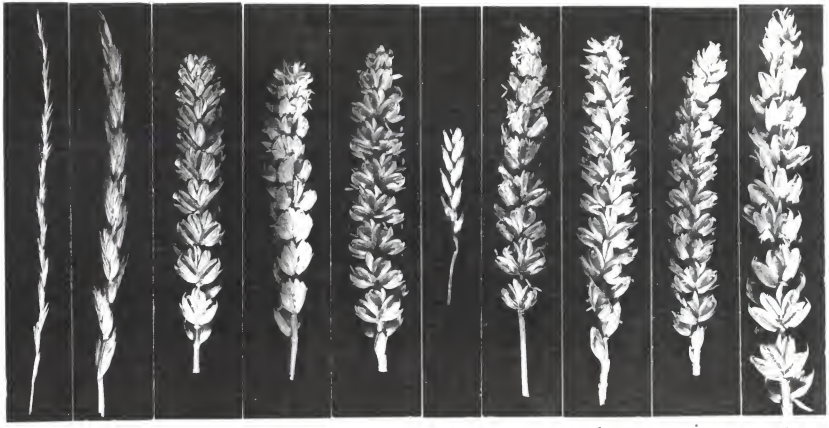
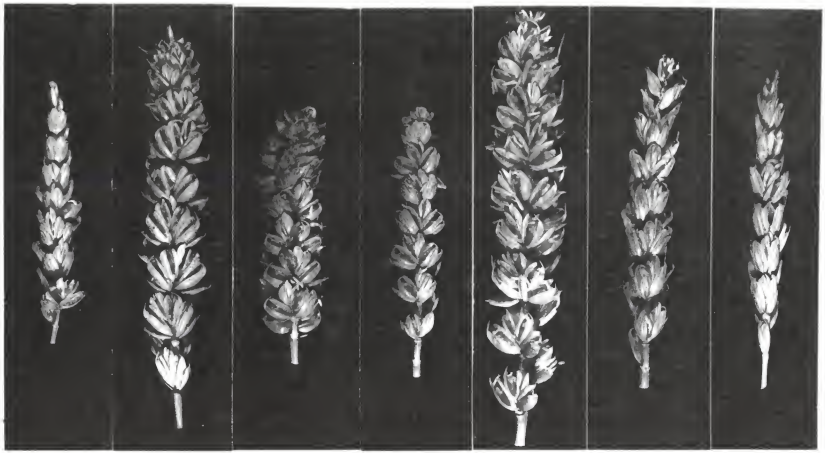

a
b
c
d
e
f
g
h
i
j

Figure 17. Spike morphology of (a) disomic addition $7H^tp$, (b) disomic addition $7S^t$ del, (c) disomic substitution $1H^tp$-5A(5A), (d) disomic substitution $4S^tq$.7Aq(7A), (e) disomic addition $1H^tp.7S^tp$, (f) disomic addition $1H^tp.5H^tq$, (g) double monoditelosomic addition $1H^tp$.(?), $1H^tp.5H^tq$, unidentified pair of *Elymus* telosomes.



a b c d e f g

Figure 18. Estimates of fertility of Chinese Spring and the addition, substitution, and translocation lines.

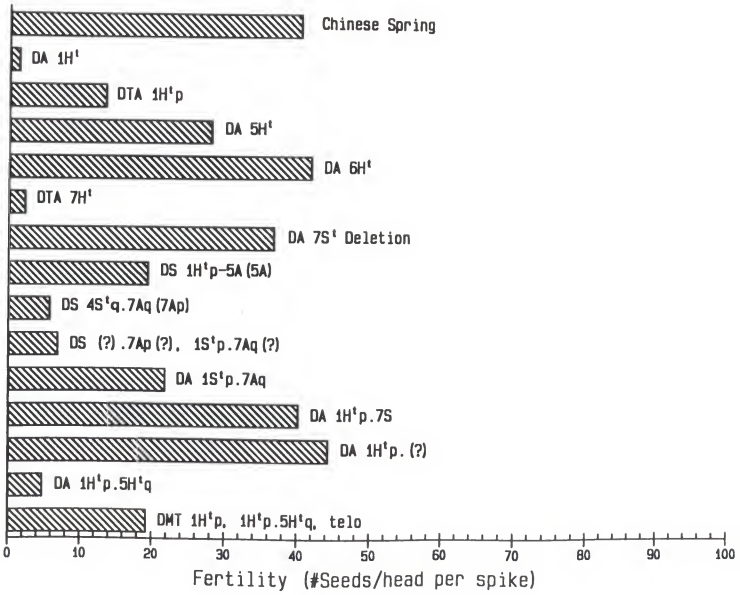
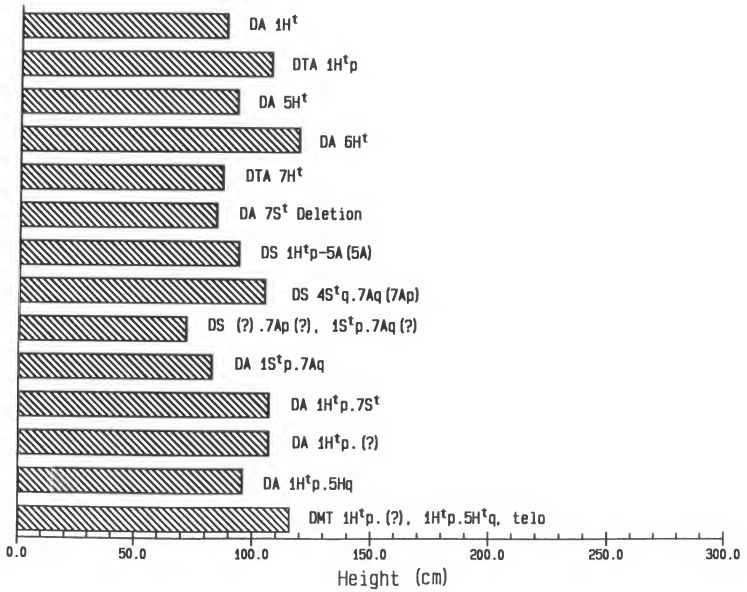

Chinese Spring
DA 1H^t
DTA 1H^{t}p
DA 5H^t
DA 6H^t
DTA 7H^t
DA 7S^t Deletion
DS 1H^{t}p-5A (5A)
DS 4S^{t}q.7Aq (7Ap)
DS (?) .7Ap (?), 1S^{t}p.7Aq (?)
DA 1S^{t}p.7Aq
DA 1H^{t}p.7S
DA 1H^{t}p. (?)
DA 1H^{t}p.5H^{t}q
DMT 1H^{t}p, 1H^{t}p.5H^{t}q, telo
0
10
20
30
40
50
60
70
80
90
100
Fertility (#Seeds/head per spike)

Figure 19. Mean plant height of the addition, substitution and translocation lines.


DA 1H^t
DTA 1H^tp
DA 5H^t
DA 6H^t
DTA 7H^t
DA 7S^t Deletion
DS 1H^tp-5A (5A)
DS 4S^tq.7Aq (7Ap)
DS (?) .7Ap (?), 1S^tp.7Aq (?)
DA 1S^tp.7Aq
DA 1H^tp.7S^t
DA 1H^tp. (?)
DA 1H^tp.5Hq
DMT 1H^tp. (?), 1H^tp.5H^tq, telo
0.0
50.0
100.0
150.0
200.0
250.0
300.0
Height (cm)

APPENDIX

Parental species *E. trachycaulus* and isolated lines were evaluated for disease resistance through cooperative investigations. *Elymus trachycaulus* was tested for reactions to leaf rust, powdery mildew, and barley yellow dwarf virus (BYDV). The isolated lines were screened for resistance if the parental species was found to be resistant to a specific disease.

Leaf Rust

Leaf rust resistance was determined by Dr. L.E. Browder, USDA-ARS, Kansas State University, Manhattan, KS. Two to three-leaf seedlings were tested for reactions to *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* cultures PRTUS1, PRTUS2, PRTUS3, PRTUS4, PRTUS5, PRTUS6, PRTUS7, PRTUS8, PRTUS14, PRTUS15, PRTUS21, PRTUS24, PRTUS25, and PRTUS28 with the urediospore-oil suspension inoculation method described by Browder (1971). Infection types were observed 10-12 days after inoculation and coded according to the system of Browder and Young (1975). The first code portrays relative sporulation on a scale of 0-9 and the second code shows relative lesion size on a scale of 0-9; the third (alphabetic) describes infection type: X = indefinite, C = chlorosis, P = pale, and N = necrosis. Scores were 000 = immune, 01C-23X = highly resistant, 56X-67X = moderately resistant, 78X-99P = susceptible.

Controls and isolated lines	Culture													
	1	2	3	4	5	6	7	8	14	15	21	24	25	28
Chinese Spring	88P	88P	88P	88P	88P	88P	88P	88P[a]	88P	88P	88P	88P	88P	88P
E. trachycaulus	13X	03C	02C	13X	02C	34X	13X		13X		23X	45X	23X	13X
Agent	13X	03C[b]	13X	13N	23X	34X	13X	23X	23N	56X	04C	56X	88P	45N
Agatha	02C	02C	13X	02C	02C		02C	01C	02C	01C	02C	02C		02C
7D/Ag #11	78X	78X[c]	02C	02C	78X	88P	88P	56X	88P	88P	88P	88P	88P	88P
DA $1H^t$	78X	88P	78X[a]	01C[b]	23X	23X[d]	88P[e]	56X	88P	56X	88P	01C[f]	24X[g]	88P
DA $1H^tp$	78X	88P	78X	88P	23X	78X	78X	56X	88P	56X	88P	88P	56X[h]	88P
DS $1H^tp$-5A(5A)	78X	78X	78X	78X	45X	78X	78X[b]	56X	88P	78X	23X[h]	88P	56X	88P
DA $1H^tp.7S^t$	78X[b]	88P	78X[a]	01C[b]	34X	78X	78X	56X[a]	88P	56X	88P	88P	45X[d]	88P
DA $7S^t$ del	88P	88P	88P	01C[b]	88P	88P	88P	88P	88P	88P	88P	88P	88P	88P
DA $1H^tp.(?)$	78X[b]	78X	78X[b]	78X	23X	78X[b]	78X[b]	56X[b]	88P	56X	88P	88P	23X[i]	88P
DMTA $1H^tp.(?)$, $1H^t.5H^tq$, unidentified Elymus telosomes	78X	88P	78X	78X[b]	78X	78X	78X	56X	88P	56X	88P	88C	88C	88C
DA $5H^t$						88P							88P	
DA $6H^t$						88P							88P	
DS $4S^tq.7Aq(7A)$						88P							88P	

[a] Low infection density on all plants.
[b] Also segregating for infection type 88P.
[c] Also segregating for infection type 03C.
[d] Also segregating for infection types 56X and 78X.
[e] Second leaf showed infection type 78X.
[f] Also segregating for infection types 56X and 88P.
[g] Also segregating for infection types 34X, 45X, and 56X.
[h] Also segregating for infection types 78X and 88P.
[i] Also segregating for infection types 56X, 78X, 88C, and 88P.

Powdery Mildew

Powdery mildew resistance was determined by Dr. J. G. Moseman, USDA-SEA, Beltsville, MD. Plants were screened for resistance to *Erysiphe graminis* DC. ex Merat f. sp. *tritici* em Marchal composite culture: ABK, Asosan, and Yuma/CC (Moseman *et al.* 1983; Tomerlin *et al.* 1984). Reactions for infection type were read 7-9 days after inoculation on a scale of 0-9, where 0 = immune, no visible signs of infection, 1-3 = highly resistant, 4-6 = moderately resistant, and 7-9 = susceptible.

Results:

Parental materials and isolated lines	ABK, Asosan, and Yuma/CC
Chinese Spring	9
E. trachycaulus	4
DA $1H^t$	4-6
DA $1H^tp$	9
DA $1H^tp.(?)$	9
DA $5H^t$	6
DA $6H^t$	8
DS $4S^tq.7Aq(7A)$	9
DS $(?).7Ap(?) + 1S^tp.7Aq(?)$	9

Barley Yellow Dwarf Virus

Evaluation for barley yellow dwarf virus (BYDV) resistance was performed by Dr. R.M. Lister, Purdue University, West Lafayette, IN. BYDV isolates, PAV (virus nonspecifically transmitted by *Rhopalosiphum padi* and *Macrosiphum avenae*), RPV (virus specifically transmitted by *R. padi*), and MAV (virus specifically transmitted by *M. avenae*) were used in transmission tests described by Rochow (1982). An enzyme-linked immunosorbent assay (ELISA) was employed on test plants and controls to verify their virus status (Rochow 1982). An ELISA reaction was considered positive if the absorbance value was greater than that of the healthy controls.

Results:

Parental materials and isolated lines	Isolate		
	PAV	RPV	MAV
Chinese Spring	S	S	S
E. trachycaulus	S	R	R
DA $1H^t$	S	S	S
DA $1H^tp$	S	S	S
DA $1H^tp.(?)$	S	S	S
DA $5H^t$	S	S	S
DA $6H^t$	S	S	S
DA $1H^tp.7S^tp$	S	S	S
DS $4S^tq.7Aq(7A)$	S	S	R
DS $(?).7Ap(?) + 1S^tp.7Aq(?)$	S	S	S

Isolation and Characterization of Wheat-*Elymus* Addition, Substitution, and Translocation lines

by

KAY DUFFENS MORRIS

B. S., Kansas State University, 1982

AN ABSTRACT OF A THESIS

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ABSTRACT

A combination of cytological methods were used to isolate and identify fourteen addition, substitution, or translocation chromosomes from tetraploid *Elymus trachycaulus* ($S^tS^tH^tH^t$) in Chinese Spring wheat. Characterization of these lines indicate that at least seven *Elymus* chromosomes or telosomes of $1H^t$, $5H^t$, $6H^t$, $7H^t$, $1S^t$, $4S^t$, and $7S^t$ have been either added or incorporated (as translocations) into the wheat genome. Several alloplasmic lines were recovered in which three different *Elymus* chromosomes showed varying effects on vigor and fertility restoration within the same *Elymus* cytoplasm. Genetic analyses of translocated or *Elymus* chromosomes from euplasmic multiple, monosomic, or monotelosomic addition lines indicate that the transmission frequencies of most chromosomes ranged from 0% to 11%, with the exception of three chromosomes which showed preferential transmission through the male or female gametes. The translocated or *Elymus* chromosomes of each line were found to have an effect on plant morphology with the exception of disomic addition $6H^t$ which appeared similiar to Chinese Spring. This may be attributed to the expression of genes from specific *Elymus* chromosomes or nucleo-cytoplasmic interactions. Moreover, *Elymus* chromosomes $7H^t$ and $7S^t$ were identified as carrying genes for anthocyanin production. These morphological traits in

combination with biochemical markers as identified from previous studies provide evidence of gene synteny relationships between the *Elymus* and *Triticum* species. Knowledge of the homoeologous relationships among wheat and *Elymus* chromosomes may be useful for the eventual transfer of disease resistant genes from several wheat-*Elymus* addition lines into wheat.